

AD-A212 681 MENTATION PAGE

Form Approved
OAI8 No. 0704-0188

1a. REPORT SECURITY CLASSIFICATION UNCLASSIFIED		1b. RESTRICTIVE MARKINGS NONE	
2a. SECURITY CLASSIFICATION AUTHORITY DTIC ELECTE		3. DISTRIBUTION/AVAILABILITY OF REPORT Approved for public release; distribution Unlimited.	
2b. DECLASSIFICATION/DOWNGRADING SCHEDULE 20 1989		5. MONITORING ORGANIZATION REPORT NUMBER(S)	
4. PERFORMING ORGANIZATION REPORT NUMBER(S) D		7a. NAME OF MONITORING ORGANIZATION Walter Reed Army Institute of Research	
6a. NAME OF PERFORMING ORGANIZATION Department of Medical Neurosci. Div. of Neurosensitivity	6b. OFFICE SYMBOL (If applicable) SGRD-UW1-B	7b. ADDRESS (City, State, and ZIP Code) Washington, DC 20307-5100	
6c. ADDRESS (City, State, and ZIP Code) Walter Reed Army Institute of Research Washington, DC 20307-5100		9. PROCUREMENT INSTRUMENT IDENTIFICATION NUMBER	
8a. NAME OF FUNDING/SPONSORING ORGANIZATION US Army Medical Research and Development Command	8b. OFFICE SYMBOL (If applicable)	10. SOURCE OF FUNDING NUMBERS	
8c. ADDRESS (City, State, and ZIP Code) Ft. Detrick Frederick, MD 21701		PROGRAM ELEMENT NO. 61102A	PROJECT NO. 3M161102BS
		TASK NO. 10 CD	WORK UNIT ACCESSION NO. 213
11. TITLE (Include Security Classification) Performance of a Weight-Lifting Task by Normal and Deafferented Monkeys			
12. PERSONAL AUTHOR(S) Wylie, Richard M. and C.F. Tyner			
13a. TYPE OF REPORT	13b. TIME COVERED FROM _____ TO _____	14. DATE OF REPORT (Year, Month, Day)	15. PAGE COUNT
16. SUPPLEMENTARY NOTATION			
17. COSATI CODES		18. SUBJECT TERMS (Continue on reverse if necessary and identify by block number)	
FIELD	GROUP	SUB-GROUP	
		Primates, Motor Control, Deafferentation, Movement, Eye-Hand Co-ordination	
19. ABSTRACT (Continue on reverse if necessary and identify by block number)			
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20. ABSTRACT SECURITY CLASSIFICATION UNCLASSIFIED		21. ABSTRACT SECURITY CLASSIFICATION UNCLASSIFIED	
22. DISTRIBUTION STATEMENT UNCLASSIFIED		23. DISTRIBUTION STATEMENT UNCLASSIFIED	
24. DISTRIBUTION STATEMENT UNCLASSIFIED		25. DISTRIBUTION STATEMENT UNCLASSIFIED	

Performance of a Weight-Lifting Task by Normal and Deafferented Monkeys

Richard M. Wylie and C. F. Tyner

Department of Medical Neurosciences
Walter Reed Army Institute of Research, Washington, DC

The role of topographic information from a moving limb in controlling the trajectory of the limb was explored by comparing the ability of 3 normal and 2 unilaterally deafferented monkeys to generate criterion elbow flexions when opposed by different weights. When lifting initially unknown weights, both groups of monkeys reached maximum positions that were inversely related to load. The performance of the deafferented monkeys approached that of the normal monkeys on these first lifts of initially unknown weights. The preceding load had a greater effect on the initial lifts of the deafferented monkeys than on those of the normal monkeys. When allowed to repeatedly lift the same weight, both groups obtained a high density of reinforcement, but the responses of the deafferented monkeys were more dependent on the weight. The results are consistent with the hypothesis that the mechanical properties of muscle make an important contribution to compensation.

The mechanisms underlying the control of a moving limb are poorly understood. The assumption that topographic information arising from the sensory system of the moving limb plays an important role in controlling the evolving trajectory has been challenged by the performance of deafferented monkeys (Bizzi, Dev, Morasso, & Polit, 1978; Gorska & Jankowska, 1959; Knapp, Taub, & Berman, 1963; Polit & Bizzi, 1979; see Taub, 1977, for review). Recent work on head turning (Bizzi et al., 1978) and arm positioning (Polit & Bizzi, 1979) has indicated that the mechanical properties of activated muscles, particularly under conditions of co-contraction of the antagonists acting at a joint, play an important role in the response to perturbations. Bizzi and his co-workers postulated that as a consequence of the mechanical properties of the musculo-skeletal system, the nervous system can specify a final position independent of knowledge of the initial position. Because the neural signals driving the muscles must inevitably undergo a transformation through the mechanical properties of muscle, one must assess the relative contributions of the mechanical properties of muscle and of the sensory signals arising from the moving limb to the trajectory.

We have explored the role of topographic sensory information in movement by comparing the performances by normal and unilaterally deafferented monkeys of an elbow flexion task in which reinforcement was contingent upon flexing the forearm in the vertical plane through a criterion arc against different external gravitational loads. In this study we focused on the maximum heights achieved by the two

groups of monkeys to establish the degree to which the performance of deafferented monkeys approaches that of normal monkeys. We have presented preliminary reports (Wylie & Tyner, 1978, 1981), arguing that the ability of deafferented monkeys to compensate for an unknown external load during an ongoing lift underlies part of the performance to be described in this article.

It is important to bear in mind two unresolved issues: (a) the problem of residual sensation from ventral root afferents, spared dorsal roots, or regenerated dorsal roots (to date, there is no evidence that residual sensation plays a role in recovery of function after dorsal rhizotomy; Bizzi et al., 1978; Polit & Bizzi, 1979; Taub, Hager, Grier, & Hodos, 1980; Wylie, Barro, & Taub, 1979) and (b) the problem of whether a particular motor task per se requires topographic sensory information. In this article we argue that the performance of deafferented monkeys on a weight-lifting task approaches that of normal monkeys but that the differences between the two groups reflects the contribution of topographic feedback to the performance of the normal animals and that the results are consistent with the assumption that dorsal rhizotomy suffices to abolish topographic sensory information.

Method

Subjects

Five male Rhesus monkeys (*Macaca mulatta*) were used in this study. Three served as normal controls, and 2 underwent unilateral dorsal rhizotomies to eliminate afferent inputs from the upper extremity destined to perform the weight-lifting task. The animals were housed in individual cages and transported to the experimental apparatus for 90-min sessions each working day. Monkey chow supplemented with fresh fruit was provided at the end of each day. The amount of food each monkey received was controlled to maintain high rates of responding during the experimental session but was sufficient to maintain growth. Each animal was provided with a liter of water at feeding time which was usually consumed by the start of the next day. Both deafferented monkeys were naive at the time

We thank Leon Butler, James Morrison, and John Oubre for technical assistance, Charles Gernand for construction of the apparatus, the staff of the Division of Biometrics, Walter Reed, for computer programming, and Annabelle Trees for the art work.

Correspondence concerning this articles should be addressed to Richard M. Wylie, Department of Medical Neuroscience, Walter Reed Army Institute of Research, Washington, DC 20307.

of surgery. Deafferentations were performed under anesthesia and sterile conditions. Dorsal roots C2-T4 innervating the right upper extremity were sectioned intradurally, with the dorsal root ganglia being spared. Care was taken to avoid damaging radicular blood vessels, but minor bleeding inevitably occurred, indicating some damage. Any ventral root afferents with ganglion cells in either the dorsal root ganglia or the ventral roots are presumed to be intact. Training was begun 2-3 months postoperatively, after all surgical wounds had healed.

Procedure

Apparatus. The monkeys were restrained on a perch by a yoke around the neck and placed in the experimental apparatus. In the apparatus, straps restrained both upper arms against fixed blocks. Each forearm was restrained by a metal cuff fastened to a lever arm with its center of rotation at the elbow. Movement was thus constrained to flexion of the forearm in the vertical plane. A mechanical stop supported each forearm and its restraint when the forearm was in the horizontal rest position. In this rest position, the angle between the upper arm and the lower arm was about 140°. A second mechanical stop limited the maximum flexion of the arm to an angle of 60°. The weights were discrete masses that were suspended from the arm restraint by a chain and generated no load on the monkey when the arm was in the rest position. The weights hung in a well, out of sight of the monkey. The chain passed over guides arranged so that as the arm restraint was rotated, the chain followed the arc described by the lever arm, and the direction of pull remained vertically over the weight. The lever arm was 23.4 cm. The chain and hanger weighed 114 g and constituted a gravitational resistance in addition to that of each weight. As the arm rotated, the contribution of the chain to the gravitational force acting on the system decreased in proportion to the arc of rotation. A maximum excursion of the arm would transfer 20.6 g from the combined mass of chain, hanger, and test load to the rotating mass of the arm restraint and arm. This is a negligible change given the range of weights used and has been ignored. The mass of the arm restraint and lever were balanced with a counterweight so that the center of gravity of these constant components of the system would coincide with the center of rotation. The total mass of the arm restraint, lever arm, and counterbalance was 1,390 g, with an estimated rotational inertia of 300,000 gcm². As developed elsewhere (Wylie & Tyner, 1981), the constant masses associated with the monkey's arm and the apparatus constitute a significant part of the total load manipulated by the monkey in performance of the task.

The rotation of the arm restraint was coupled to a rotary position encoder which generated a voltage proportional to the arm position. The position signal was electronically differentiated to record velocity and acceleration. These signals were displayed on an ink-writer and also sampled at 100 Hz and stored in binary format on magnetic tape for off-line computer analysis.

Digital logic circuits were used to control reinforcement. Computer processing provided measurements of the variables of motion (position, velocity, and acceleration) as functions of time. Peak-height distribution histograms were plotted for every trial. The computer printouts included the mean peak position achieved on each trial and its standard deviation, the peak height of first and successive lifts, and measurements of the trajectory of the arm at different times after the start of a lift. In this article we concentrate on the highest position achieved on first lifts of an initially unknown weight, the highest position achieved on successive lifts of the same weight, and the mean peak height achieved in each trial.

Paradigm. To obtain a reinforcement, the monkey had to initiate a response by flexing its non-weight-lifting arm to trip a microswitch. This triggered two temporal windows. The first determined the pe-

riod within which the monkey had to flex the weight-lifting arm to the criterion position, and the second determined the period within which the monkey had to return its arm to rest. The first temporal window started 0.25 s after the trigger and lasted 1 s. The second temporal window began 0.75 s after the trigger and also lasted 1 s. The criterion flexion was about 40°, raising the weight vertically about 16.5 cm. All lifts that exceeded the criterion height and returned to rest within the temporal constraints were reinforced with a liquid nutrient (Sustagen, Mead Johnson, dissolved in water). Reinforcements were delivered after the arm had returned to the rest position, and no external cue was provided to signal crossing of the criterion level. The experiments were carried out in a closed but illuminated booth in the presence of masking noise to reduce the effect of extraneous sounds. The monkeys had full view of their arms. It should be emphasized that this task inevitably generates cues that might contribute to performance: In addition to vision, movement generates sounds, load-dependent stresses may be transmitted to intact regions of the body, and so on. Consequently, the experiments should be interpreted as comparing the performance of animals with normal topographic information from the responding limb with the performance of those lacking this topographic information consequent to dorsal rhizotomy but with all other potential sensory channels intact.

Testing. All animals were initially trained to perform the position task in the absence of any external load. In order to obtain measures of normal baseline performance, the 3 normal animals were run through an ascending series of weights ranging from about 100 g to the highest weight at which each individual animal would consistently perform. During this phase of the study, the loads remained constant during each 90-min daily session, and the animals were run for 1-2-week periods on each load. We performed the first deafferentation (Scrub) after establishing boundaries on the performance of normal animals. We performed the second deafferentation (Mutt) after obtaining preliminary results from Scrub. A preliminary test with the first deafferented animal indicated that changing from no external load to the lowest weight in the series (114 g) had negligible effect on performance, and we consequently established a moderate load (459 g) as a more appropriate initial challenge. This load impaired the performance of both deafferented animals, largely consequent to the effects of muscle fatigue (Wylie, 1978). Both monkeys were run at the same moderate load for a number of months until their daily performances approached those of normal animals before beginning the test procedures used in this study. Two distinct test procedures were used to obtain the data presented here. In one, the daily weight-change paradigm, the weight remained constant throughout the 90-min session but was changed from day to day. In the second test procedure, the 5-min weight-change paradigm, the daily session was divided into fifteen 5-min trials. Between trials, the experimenter replaced the previous weight with the next scheduled weight, manually restrained the monkey from premature lifting, and after starting the new trial, released the monkey's arm. A block of sessions spanning 7-13 days constitutes one replication of the 5-min weight-change paradigm, and the data from each replication for each animal constitute a single set of data. Either training or test sessions in the daily weight-change paradigm separated successive replications of the 5-min weight-change paradigm by periods from several months to as long as a year. Scrub was initially tested in the daily weight-change paradigm with three weights (114, 291, and 414 g). In the final phase of testing, he was tested in the 5-min weight-change paradigm over the same range of weights. The protocols for Mutt were somewhat revised in light of our results from Scrub. After Mutt reached asymptotic performance levels at 459 g, he was tested in the 5-min weight-change paradigm over the same range as Scrub had been tested (114, 291, and 414 g). In contrast to Scrub, Mutt's first experience in the 5-min weight-change paradigm was also his

first experience with those test loads. After this test, he was then given practice runs with the same weight daily and retested in the 5-min paradigm over a more extensive range of weights (114, 291, 414, and 608 g). Then he was tested in the daily weight-change paradigm and finally retested in the 5-min paradigm across the more extensive range of weights. Scrub was tested in the 5-min paradigm by alternating test trials with trials at a standard load (114 g). Mutt was run on a pseudorandom schedule of weight changes in which on each day all weights were presented an equal number of times but in an unpredictable order. The normal animals were run through similar sets of trials to provide normal comparisons with each of the experimental animals. In the 5-min weight-change paradigm, the first trial of each day was treated as a "warming-up" trial, and the results are not included in the data presented.

Results

Normal Baseline

The normal monkeys worked throughout 90-min sessions with loads ranging from about 100 g to more than 1,100 g. For each animal, there was a maximum load above which the animal would generate only a few lifts and then cease working. The normal monkeys generated fewer lifts/session as the load was increased, but the trajectories, to a first approximation, were invariant over the entire range of loads. Inspection of the peak-height distribution histograms showed that there was a single prominent mode, with a narrow and reasonably symmetric dispersion about the mode. As the load increased, responding tended to become intermittent, with occasional long interresponse times separating runs of short interresponse times. Although the total number of responses emitted during a session fell as the load was increased, the total physical work performed on the load increased, tending asymptotically toward a maximum at the heaviest loads (Wylie, 1978). These results suggested that the confounding effects of muscle fatigue that might develop over successive lifts could be reduced by testing the deafferented animals at loads below 500 g.

Daily Weight-Change Paradigm

Comparison of session averages. Both deafferented monkeys were trained at 459 g until they reached an asymptotic performance. During the terminal 20 sessions of this training, the median percentage of correct responses (number of reinforcements/responses initiated) for Scrub was 86.7 and for Mutt, 82.0.

The results for all of the animals from the daily weight-change paradigm are shown in Table 1. The results from each animal were tested for a significant effect of load on the percentage of correct responses by the Kruskal-Wallis test (Hollander & Wolfe, 1973), with the H statistic referred to χ^2 . We found no effect for any of the normal animals: Squirt, $H(2) = 3.728$, $p > .1$; Henry, $H(2) = 2.471$, $p > .25$; Jeff, $H(2) = 2.025$, $p > .25$. In contrast, the results for both of the deafferented monkeys showed a significant effect: Scrub, $H(2) = 9.723$, $p < .01$; Mutt, $H(3) = 16.252$, $p < .01$. A one-way analysis of variance performed on the mean maximum heights generated by each animal across loads revealed that load had no effect on the mean heights generated by the

Table 1
Percentage of Correct Responses and Maximum Heights at Each Load

Animal and load (in g)	N	Q_1	Median	Q_3	Height (in cm)
Normal					
Squirt					
114	13	79.1	82.0	87.0	16.4 \pm 0.1
291	16	82.0	86.0	90.4	16.6 \pm 0.1
414	17	84.2	87.8	91.9	16.4 \pm 0.1
Henry					
114	13	87.7	89.8	91.7	16.6 \pm 0.1
291	17	89.8	91.4	92.8	16.7 \pm 0.1
414	17	89.2	92.3	94.0	16.7 \pm 0.1
Jeff					
114	13	96.7	98.5	99.7	17.2 \pm 0.2
291	19	96.3	98.9	99.1	17.4 \pm 0.1
414	14	92.7	98.3	99.2	17.0 \pm 0.1
Deafferent					
Scrub					
114	7	98.6	98.9	99.4	20.0 \pm 0.6
291	9	98.0	98.2	98.7	19.1 \pm 0.4
414	10	95.1	95.8	97.8	18.3 \pm 0.3
Mutt					
114	9	94.4	96.6	97.8	21.3 \pm 0.4
291	9	93.7	98.0	98.1	19.7 \pm 0.4
414	11	81.8	87.4	90.6	19.1 \pm 0.3
608	10	85.6	87.2	90.0	19.4 \pm 0.4

Note. N = number of sessions; Q_1 and Q_3 are first and third quartiles. Heights are means \pm SE.

normal animals: Squirt, $F(2, 43) = 1.243$, $p > .05$; Henry, $F(2, 44) = .557$, $p > .05$; Jeff, $F(2, 43) = 2.155$, $p > .05$. In contrast, load did have a significant effect on the mean heights generated by both deafferented monkeys: Scrub, $F(2, 23) = 4.092$, $p < .05$; Mutt, $F(3, 35) = 6.885$, $p < .005$, heavier loads being associated with lower mean peak heights.

Both deafferented monkeys obtained high densities of reinforcement across all loads and achieved levels of performance within those achieved by the normal monkeys. Nevertheless, increasing loads reduced the percentage of correct responses and the maximum height achieved by the deafferented monkeys in contrast to the absence of any effects of load on the performance of the normal monkeys.

Variability at fixed loads in 90-min sessions. The variability in lift heights of the normal animals was smaller than that of the two deafferented monkeys. Figure 1 illustrates the behavior of both groups of animals across selected 90-min sessions. The illustrated curves provide an indication of both within-sessions variability and day-to-day variability. For this analysis, the computer printouts of all the peak heights generated within each session were broken into blocks of about 500 responses, and the last 18 successive lifts in each block were averaged. Each point in Figure 1 represents the average of these 18 sequential lifts, with its attendant standard deviation. Because the total number of lifts varied for each session, different numbers of samples were obtained from different sessions. For each animal, only three sessions at each load from the entire set of sessions are illustrated. The illustrated sessions span the 2-3-month period of testing

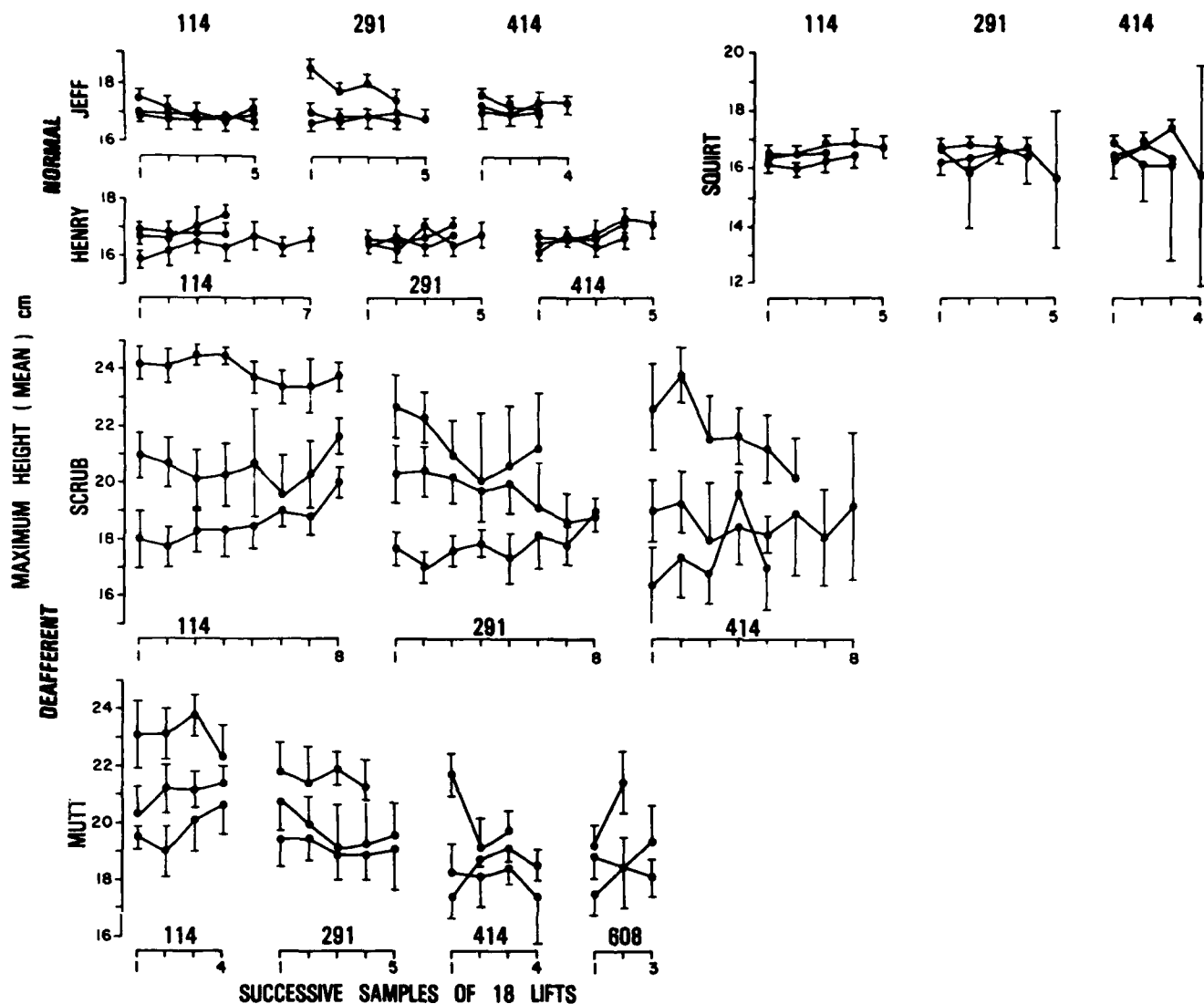


Figure 1. Effects of load on the maximum position achieved across 90-min sessions. (Each curve represents the results from a single 90-min session; each point represents the mean \pm SD of 18 consecutive lifts sampled at intervals of 500 lifts. Because the number of lifts generated within a 90-min session varies, the number of samples obtained varies from curve to curve.)

and include sessions in which the initial lifts of the session were among the lowest and highest observed. Four points emerge from inspection of Figure 1. First, with the exception of Squirt at the end of sessions with heavier loads, the variability as represented by the standard deviations is larger for the deafferented animals than for the normal animals even within 18 successive lifts. Second, on this schedule, the day-to-day variability of normal animals is considerably less than that of the deafferented animals. Third, the deafferented animals tended to develop trends across a single session so that the range of sample means within some single sessions generated by the deafferented animals exceeded the total range of means over all sessions generated by the normal animals. Finally, inspection of the curves for the two deafferented animals across loads reveals that although the peak heights

tended to decrease as the loads increased, the peak heights generated at heavier loads were often within the range of those generated at lighter loads.

To provide a more complete comparison of variability between the two groups, we obtained estimates of the lift-to-lift variability from the variance of peak heights measured in each session and of the day-to-day variability from the variance of the means from each session of the peak heights. In order to analyze the lift-to-lift variability, the average variance classified by animal and load was obtained from the variance of each session. In no case did the load have significant effect on the variance (F ratios were all less than 1.5). The session variances were therefore pooled across loads, and a mean variance for each animal was computed. The mean variances as well as the corresponding medians of the

Table 2
Mean Maximum Positions Achieved on First Lifts of Each Test Load

Animal and replication	Load (in g)				df	Slope ($\times 10^3$)
	114	291	414	608		
Normal						
Squirt						
1	14.5 \pm 0.5	13.1 \pm 0.4	10.8 \pm 0.5	—	1, 51	-13.0
2	10.9 \pm 0.6	10.3 \pm 0.5	10.1 \pm 0.6	9.4 \pm 0.6	1, 77	-2.88
Henry						
1	17.1 \pm 0.2	16.4 \pm 0.2	15.1 \pm 0.3	—	1, 58	-6.48
2	18.5 \pm 0.3	18.2 \pm 0.2	18.3 \pm 0.3	17.5 \pm 0.3	1, 96	-1.90
Jeff						
1	23.5 \pm 0.4	23.6 \pm 0.4	24.2 \pm 0.5	22.7 \pm 0.8	1, 74	-1.12
Deafferent						
Scrub						
1	16.1 \pm 0.4	15.2 \pm 0.4	14.8 \pm 0.3	—	1, 87	-4.44
Mutt						
1	22.6 \pm 0.4	19.6 \pm 0.4	18.4 \pm 0.5	—	1, 93	-14.4
2	22.1 \pm 0.5	20.4 \pm 0.5	19.9 \pm 0.6	17.9 \pm 0.7	1, 108	-8.46
3	20.4 \pm 0.3	19.5 \pm 0.4	18.0 \pm 0.5	17.8 \pm 0.5	1, 75	-5.72

Note. Values are means \pm SE expressed in centimeters.

session variances for the 3 normal animals were smaller than for the deafferented animals. In order to test for a difference between groups, a logarithmic transform was performed on the session variances, and a two-tailed t test was performed on the means of the logarithms, with $t(3) = 2.487$, $p > .05$.

The measure of day-to-day variability was extracted from the analysis of variance of the effect of load on the mean peak heights reported above (heights reported in Table 1). The residual mean squares of the normal animals were all smaller than those of the deafferented animals. A two-tailed t test on the residual mean squares yielded a significant difference between groups, $t(3) = 15.91$, $p < .001$.

Within a session, the normal animals tended to show less variability, but the overlap in variances of the normal and deafferented monkeys was sufficient to preclude finding a

significant difference. In contrast, and as reflected in Figure 1, the day-to-day variability of means for the normal animals was significantly less than that for the deafferented animals.

Five-Minute Weight-Change Paradigm

Effect of an initially unknown load. On first lifts of an initially unknown weight, all animals, normal and deafferented, generated sufficient torque to lift each of the test weights. We computed, for each animal, the mean maximum position achieved on first lifts of each test weight for each replication. In all cases, there was an inverse relation between the mean peak height and the test load. To assess the magnitude of the inverse relation for each monkey, we performed a least-squares regression of position on the test weights. The means and

Table 3
Mean Maximum Positions Achieved on 25th Lifts of Each Test Load

Animal and replication	Load (in g)				df	Slope ($\times 10^3$)
	114	291	414	608		
Normal						
Squirt						
1	16.3 \pm 0.1	16.4 \pm 0.1	16.4 \pm 0.1	—	1, 51	0.316
2	17.6 \pm 0.1	17.6 \pm 0.1	17.5 \pm 0.2	17.1 \pm 0.1	1, 77	-1.08
Henry						
1	17.9 \pm 0.2	17.5 \pm 0.1	17.3 \pm 0.1	—	1, 58	-1.73
2	19.5 \pm 0.2	19.0 \pm 0.2	19.1 \pm 0.2	18.7 \pm 0.1	1, 96	-1.48
Jeff						
1	22.5 \pm 0.3	22.3 \pm 0.3	21.9 \pm 0.3	21.6 \pm 0.3	1, 74	-2.04
Deafferent						
Scrub						
1	16.8 \pm 0.3	16.9 \pm 0.2	15.3 \pm 0.4	—	1, 87	-5.02
Mutt						
1	20.5 \pm 0.2	19.2 \pm 0.2	18.7 \pm 0.4	—	1, 93	-5.96
2	21.7 \pm 0.4	20.9 \pm 0.4	20.0 \pm 0.4	19.1 \pm 0.4	1, 108	-5.43
3	19.9 \pm 0.3	19.5 \pm 0.4	19.2 \pm 0.3	18.7 \pm 0.3	1, 75	-2.38

Note. Values are means \pm SE expressed in centimeters.

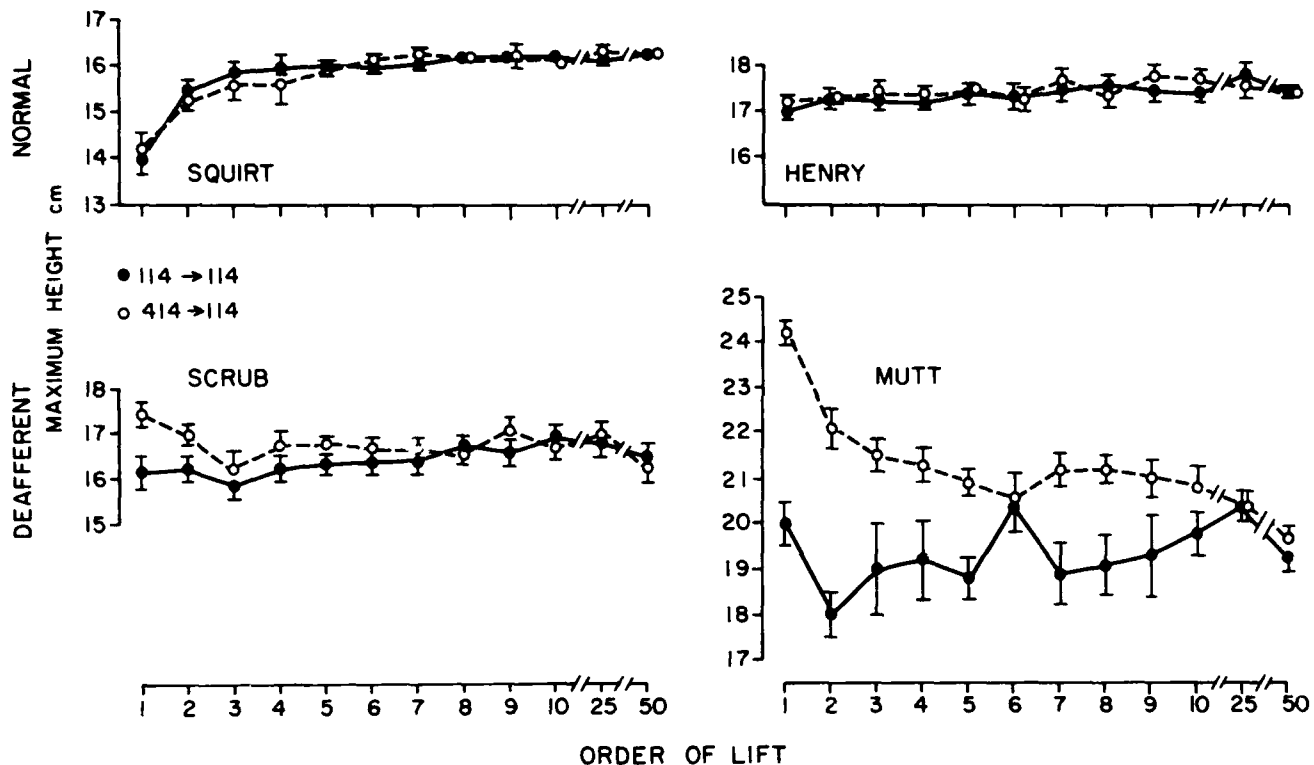


Figure 2. Effect of the preceding load on the response to the current test load. (The average maximum position is plotted against the order of lifts. In all cases, the test load was 114 g, but the preceding load was either 114 g [filled symbols] or 414 g [open symbols]. The error in estimation of the means is represented by the standard error of the mean.)

estimated slopes are presented in Table 2. At each load, the range of mean peak heights generated by the normal animals includes the means generated by the deafferented monkeys. The overlap in the slopes measured for the two groups is sufficient to conclude that the performance of the deafferented monkeys approached that of the normal monkeys.

We followed the same procedure to compare peak heights on the 25th lifts of the same weights. The mean heights, classified by load, are given in Table 3, along with the estimated slopes. All of the slopes obtained from the normal monkeys are closer to zero than those from the deafferented monkeys, which indicates that by the 25th lift, the normal monkeys were generating movements more nearly independent of the weight than were the deafferented monkeys.

The first lifts of an unknown load generated by both groups were inversely related to load. We found no quantitative difference between groups in the slopes measuring this inverse relation. After repetitive lifts of the same load, the normal animals showed a weaker inverse relation. In contrast, the slopes measured for the deafferented monkeys on 25th lifts were about the same as on their first lifts.

Effect of preceding loads and the central tendency. When initial lifts on a trial generated by deafferented monkeys deviated very much from some central tendency, later lifts tended toward that central tendency. As documented in this section, the load on the trial immediately preceding any test

trial tended to perturb the response to the test loads. Examples of this perturbation are illustrated in Figure 2. In Figure 2, the average peak heights achieved over successive lifts at a test load of 114 g is separated in terms of the preceding load. On first lifts of 114 g, both deafferented monkeys lifted higher when the test load was preceded by 414 g than when it was preceded by 114 g. The heights of successive lifts at 114 g when preceded by 414 g converged on those generated when the test load was preceded by itself. In the examples illustrated in Figure 2, the effects of the preceding loads on the responses of the two normal animals to the test load were at best small. To examine the effects of the preceding loads on the response to test loads, we performed a least-squares regression analysis on each replication for each animal, to obtain the slope of the regression of maximum position on first lifts on the preceding load. For those replications in which 114 g was alternated between test loads, we obtained the regression of lift heights measured on trials at 114 g on the preceding test loads. For replications in which the loads were presented quasi-randomly, we obtained the regression of all first lifts on the preceding test loads. The mean peak heights and the regression coefficients measuring the slopes of the regression lines are presented in Table 4. In all cases, the regression coefficients were positive, which indicates that the preceding load had an effect on both groups, but the coefficients for the deafferented animals were all more

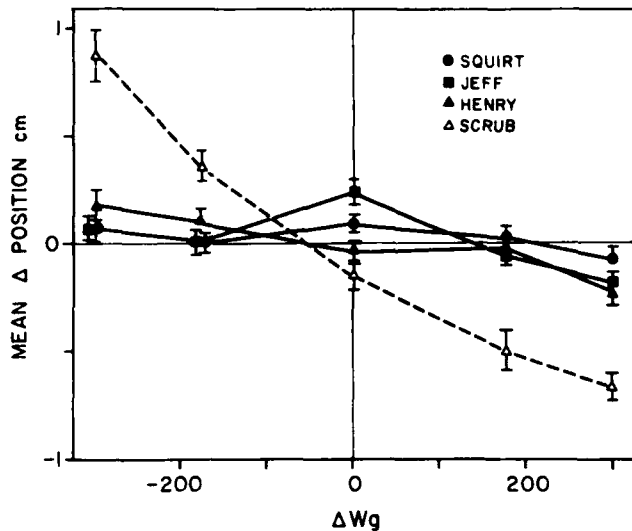


Figure 3. Comparison of the effects of load on the trial averages of position between 3 normal monkeys (filled symbols) and 1 deafferented animal (Scrub, open symbols). (The mean \pm SE differences between positions are plotted against the differences between loads on successive trials taken across all of the test days. The test loads [114, 291, 414 g] were alternated between trials at a standard load [114 g], with the consequence that zero and negative weight changes indicate a change from one of the test loads to the standard of 114 g and the positive changes represent a change from 114 g standard to one of the two heavier loads.)

positive than those for the normal animals. Because the five slopes measured for the normal animals were all positive, we conclude that the preceding load affected the response of the animals to the test load. Quantitatively, the effect was greater for the deafferented animals.

The effects of the preceding load on the response to the

test load were sufficient to affect the trial averages. For this analysis, the average peak height of all lifts generated in each 5-min trial was obtained. Inspection of the results revealed that any systematic effects of load were in part obscured by the variability in the means between animals, day-to-day variability in the means generated by each animal, and the existence of trends in the means across trials conducted on a single day. In order to better isolate the effects of loads, differences were taken between the averages of successive trials within a day. The averages of these differences from all animals are plotted in Figures 3 and 4. Figure 3 shows Scrub's performance (segmented curve) and those of the normal monkeys (solid curves). In this series, a standard load of 114 g was presented between unpredictable loads, and the differences between mean heights are plotted against the differences between the corresponding loads. All increases in load represent a change from 114 g to either 291 or 414 g, all decreases represent a change from one of the heavier loads to 114 g, and 0 represents trials in which 114 g preceded 114 g. The results for the deafferented monkey show that he responded to decreases in load by increasing lift height and to increases in load by decreasing lift height. The quantitative effects of changes in the load on the performance of the deafferented monkey were more systematic and of greater magnitude than on the performance of the normal monkeys.

Figure 4 illustrates similar results obtained in a comparison of the 3 normal animals with the second deafferented animal (Mutt, second replication). In this series, the loads spanned the range from 114 to 608 g and were changed on a pseudorandom schedule. Four sets of curves are plotted, each set corresponding to one of the preceding loads and the differences plotted against the test load. As in the preceding case comparing Scrub with the 3 normal animals, this comparison shows a steeper inverse relation between load and position for Mutt than for the normal monkeys.

Table 4
Effects of Preceding Loads on First Lifts

Animal and replication	Load (in g)				df	Slope ($\times 10^3$)
	114	291	414	608		
Normal						
Squirt						
1	14.0 \pm 0.3	14.8 \pm 0.3	14.2 \pm 0.4	—	1, 60	1.15
2	10.3 \pm 0.7	9.9 \pm 0.5	10.0 \pm 0.6	10.3 \pm 0.5	1, 77	0.0286
Henry						
1	17.0 \pm 0.2	17.1 \pm 0.2	17.2 \pm 0.2	—	1, 54	0.530
2	17.5 \pm 0.3	18.2 \pm 0.3	18.0 \pm 0.3	18.6 \pm 0.2	1, 96	1.95
Jeff						
1	22.6 \pm 0.8	23.7 \pm 0.4	23.7 \pm 0.4	23.9 \pm 0.4	1, 74	2.54
Deafferent						
Scrub						
1	16.1 \pm 0.4	17.1 \pm 0.2	17.4 \pm 0.3	—	1, 73	4.33
Mutt						
1	18.6 \pm 0.4	20.1 \pm 0.5	22.3 \pm 0.5	—	1, 93	12.1
2	18.9 \pm 0.9	19.5 \pm 0.6	20.3 \pm 0.6	21.2 \pm 0.5	1, 108	4.84
3	18.2 \pm 0.6	18.3 \pm 0.4	18.8 \pm 0.4	19.9 \pm 0.4	1, 75	3.59

Note. Values are means \pm SE expressed in centimeters.

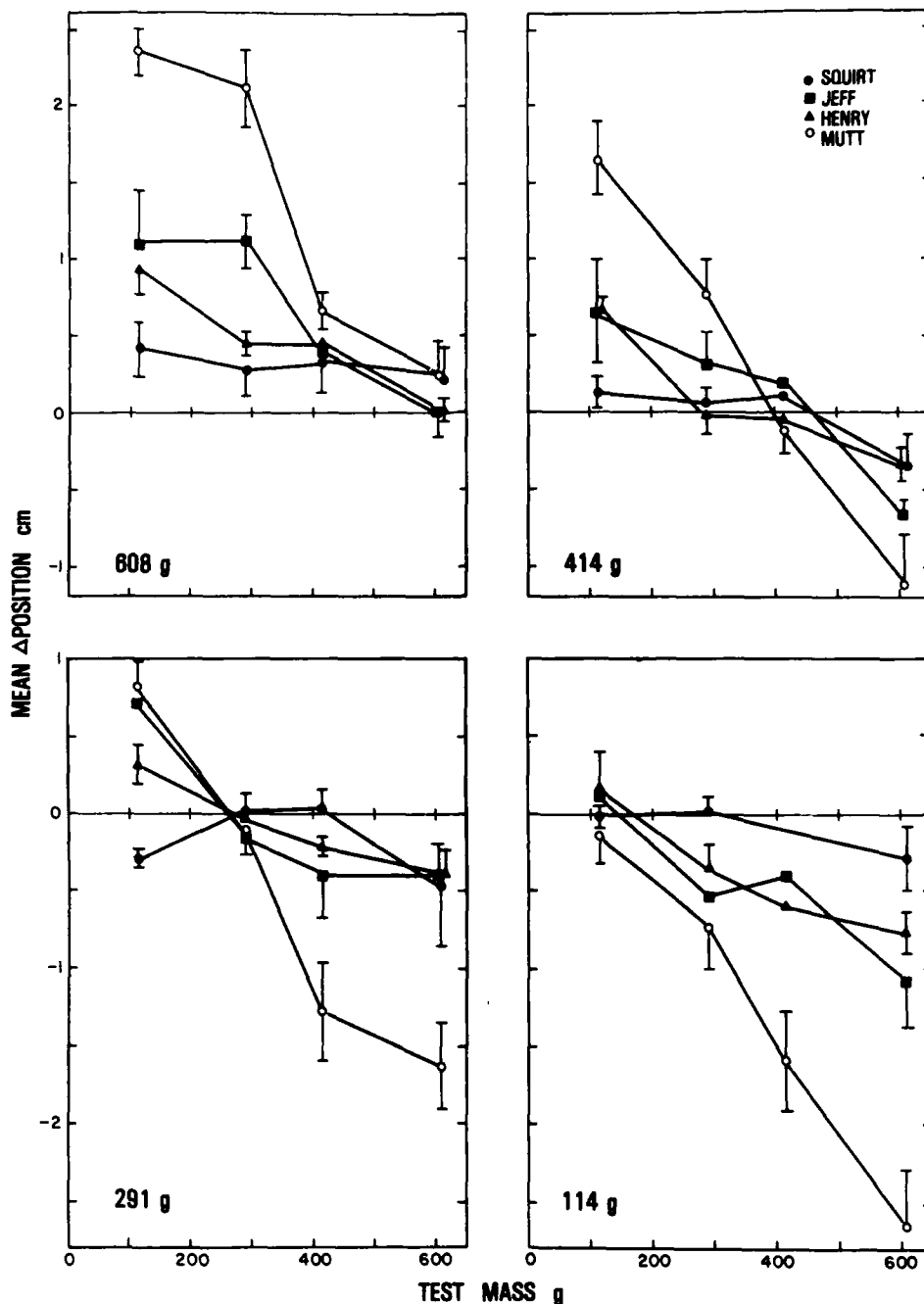


Figure 4. Comparison of the effects of load on the 5-min trial averages of position between the 3 normal animals (filled symbols) and the second deafferented animal (Mutt, open symbols). (As in Figure 3, the mean \pm SE differences between successive trial means are plotted against the differences between successive loads. (Because each test load was preceded by each load in the series, the results have been separated into four panels according to preceding load, and the differences between successive average positions are plotted against the test load.)

Discussion

Our results demonstrate that deafferented monkeys can perform not only a position task but also one confronted with unknown gravitational loads. Over the range used in this study,

they can achieve a distribution of peak heights sufficiently above criterion that the perturbing effects of different loads do not impair their ability to achieve high densities of reinforcement. On first lifts of initially unknown loads, we found no evidence of differences between groups in the steep-

ness of the regression lines relating maximum height to the test load. This interpretation depends upon the assumption that for each group, each estimate of slope represents an independent sample from the same population. It is important to note that the least negative slopes from the normal animals were from replications across the widest range of loads used and that for 2 of the normal animals (Squirt and Henry), these replications followed the earlier replications. We cannot exclude the possibility that either the addition of the heavier load or the added practice lead to less negative slopes. A more cautious interpretation of our results is that on first lifts, the performance of the deafferented animals approaches that of the normal animals. All of our evidence for subsequent lifts of the same weight in the 5-min trials indicates that the peak heights achieved by the normal animals are more nearly independent of load than those achieved by the deafferented animals. Preceding load had a stronger effect on the lifts generated by deafferented animals than on those generated by normal animals. These results were obtained in an environment rich in sensory information other than that from the responding limb and imply that sensory input from the responding limb plays an important role in maintaining accuracy in the performance of a repetitive motor task by normal animals. Although our study does not directly exclude a contribution of residual sensation from the presumably deafferented limb to the performance observed, the inability of the deafferented monkeys to match the performance of normal animals is consistent with the assumption that dorsal rhizotomy suffices to functionally deafferent a limb. The deficits we have identified are a delay in applying compensatory forces (Wylie & Tyner, 1981); a failure to apply, at the time of maximum acceleration, compensatory forces proportional to the load (Wylie & Tyner, 1981); the effects of load on peak position described here; the effects of the preceding load on the response to the current load (Figures 2, 3, and 4; Table 4); the increased variability described here; and difficulty in adapting to the problem of muscle fatigue (Wylie, 1978).

Previous studies have demonstrated that monkeys can use deafferented limbs to perform position tasks in which the target position was randomly varied (Polit & Bizzi, 1979; Taub, Goldberg, & Taub, 1975). Polit and Bizzi reported that deafferented animals could achieve the final target position even when the initial position of the arm was perturbed. Bizzi and his colleagues proposed a spring-mass model of movement in which a target position can be specified solely by specifying the equilibrium conditions appropriate for the target position; under this hypothesis, the initial position of the arm need not be known (Bizzi et al., 1978; Polit & Bizzi, 1979). Our paradigm differs in important respects from paradigms involving pointing at targets, particularly in that in our paradigm both the initial position and the criterion arc remained constant throughout the study but no external cue indicated the criterion position; also, in our paradigm, the peak height is an instantaneous position rather than a stationary final position. The general tendency exhibited by the deafferented monkeys in this study to generate responses inversely proportional to load even in the steady state is consistent with the spring-mass model. Except for first lifts

of an unknown weight, the normal animals exhibit a weaker inverse relation, a result suggesting that at least over successive lifts, the normal animals used sensory information from the limb to adjust the command signals issued to the muscles.

In its simplest form, the spring-mass model implies that for a given arc, an invariant set of command signals are issued to the muscles; any external load will have the consequence of perturbing the arc in the inverse relation we have observed, a simple analogy being a spring balance. A mathematical model of the weight-lifting paradigm based on the spring-mass model demonstrates that a system incorporating the mechanical properties of the musculo-skeletal system can lift the range of loads used in this study when driven by an invariant command signal (Wylie, 1980). Evidence has been presented, however, that in this paradigm, deafferented animals do, even on initial lifts of unknown loads, generate compensatory forces (Wylie & Tyner, 1981), and as illustrated in Figure 2, when the height achieved on an initial lift by a deafferented animal is perturbed as a consequence of the preceding load, successive lifts tend to move toward the central tendency. Therefore, we infer that in each preceding trial, the deafferented animals adjust their command signals to levels appropriate for that load, and when these are inappropriate for the unknown load on a new trial, the resulting lift height is in the direction predicted by the spring-mass model. Nevertheless, within a first lift and over successive lifts, parameters controlling the movement are adjusted in a direction appropriate for the new load.

In light of the spring-mass model, it is important to note that on a first lift of an unknown load, the peak heights of both groups on first lifts showed about the same inverse relation to load. This result is comparable to that obtained by Bizzi et al. (1978) in their study of head turning in normal and deafferented monkeys when opposed by an unexpected load. In our paradigm, reinforcement was contingent upon achieving a criterion level, and we found that over successive responses the normal animals generated lifts in which the inverse relation was weaker than that for deafferented animals. Thus, the sensory information available to normal animals evidently contributes to the adjustment of command signals on successive lifts. Because the normal animals generated initial lifts with an inverse relation to load that was about the same as those of the deafferented animals, any negative feedback loops dependent upon either a position- or a velocity-dependent error signal were evidently operating at a relatively low gain. For the normal animals we cannot distinguish between the two alternate interpretations that the relative independence of position on the repetitive lifts of the same load was due to either an increase of gain in feedback loops or the use of feedforward control to adjust the output to levels appropriate for the current load.

In conclusion, deafferentation by dorsal rhizotomy does not interfere with an animal's ability to generate distributions of peak heights across a range of loads such that a high percentage of lifts reach criterion levels and yield reinforcement. The data we have presented indicate that normal animals can achieve distributions of peak heights that are more nearly independent of the load than are the distributions generated by deafferented animals. The conjunction of cen-

trally programmed signals and the mechanics of the musculo-skeletal system appear to yield a system that can operate over a range of external perturbations in the absence of sensory signals from the responding limb. Sensory information, however, clearly contributes to the accuracy and the stability of the motor behavior.

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Received October 30, 1987
Accepted February 24, 1988 ■

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